

ON THE MORPHOLOGY OF THE CHROMOSOME GROUP IN BRACHYSTOLA MAGNA

WALTER S. SUTTON

Sutton, W. S. 1902. On the morphology of the chromosome group in *Brachystola magna*. *Biological Bulletin*, 4:24-39.

In this paper, Sutton reports cytological studies of grasshopper chromosomes that lead him to conclude that (a) chromosomes have individuality, (b) that they occur in pairs, with one member of each pair contributed by each parent, and (c) that the paired chromosomes separate from each other during meiosis.

After presenting considerable evidence for his assertions, Sutton closes his paper with a sly reference to its undoubted significance:

I may finally call attention to the probability that the association of paternal and maternal chromosomes in pairs and their subsequent separation during the reducing division as indicated above may constitute the physical basis of the Mendelian law of heredity. To this subject I hope soon to return in another place.

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ON THE MORPHOLOGY OF THE CHROMOSOME GROUP IN BRACHYSTOLA MAGNA

WALTER S. SUTTON

Zoölogical Laboratory, Columbia University,
October 17, 1902.

THE APPEARANCE OF BOVERI'S RECENT REMARKABLE PAPER¹ on the analysis of the nucleus by means of observations on double-fertilized eggs has prompted me to make a preliminary communication of certain results obtained in a general study of the germ-cells of the great "lubber grasshopper," *Brachystola magna*.

As will appear from a glance at the figures given in my former paper² upon the same form, the cells of *Brachystola*, like those of many amphibia, selachians and insects and certain of the flowering plants, exhibit a chromosome group, the members of which show distinct differences in size. Accordingly, one feature of this later study has been a critical examination of large numbers of dividing cells (mainly from the testis) in order to determine whether, as has usually been taken for granted, these differences are merely a matter of chance, or whether, in accordance with the view recently expressed by Montgomery,³ in regard to a certain pair of elements in the nuclei of one of the Hemiptera, characteristic size-relations are a constant

¹ Boveri, Th. (1902), "Mehrpolige Mitosen als Mittel zur Analyse des Zellkerns," *Verh. d. Phys. Med. Ges. zu Würzburg*, XXXV.

² Sutton, W. S. (1900), "The Spermatogonial Divisions in *Brachystola magna*," *Kans. Univ. Quart.*, Vol. 9.

³ Montgomery, T. H., Jr. (1901), "A Study of the Chromosomes of the Germ Cells of the Metazoa," *Trans. Amer. Phil. Soc.*, Vol. XX.

attribute of the chromosomes individually considered. With the aid of camera drawings of the chromosome group in the various cell-generations, I will give below a brief account of the evidence which has led me to adopt the latter conclusion.

In the first generation of secondary spermatogonia, which are the earliest germ-cells I have been able to obtain in *Brachystola*, certain differences in length and volume are to be seen between the members of the chromosome group. These cells, as shown in my former paper already referred to (where they are erroneously described as the last generation of primary spermatogonia), lie in the follicle without definite arrangement and are usually much flattened and distorted by mutual pressure and that of the growing spermatocysts between which they lie.

FIG. 1.

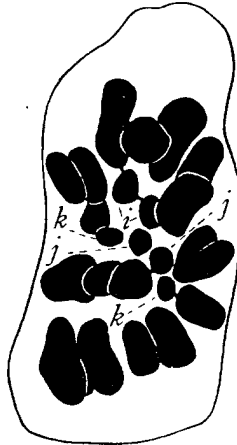


Fig. 1. Polar view of metaphase of first generation of secondary spermatogonia. Six small chromosomes designated by letters *i*, *j* and *k*. (From section.) *Note*. — All figures given in this paper are camera lucida copies of the portions under consideration from the original camera drawings to be published in the forthcoming work to which this is preliminary. The figures are not schematized.

For this reason a study of the chromosome series is difficult in this cell-generation, but, fortunately, I have been able to find a few division-figures which permit of an accurate study of the chromosomes. Such a cell as that shown in Fig. 1 — a metaphase in polar view — offers the best opportunities. Here it is apparent at a

glance that the chromosomes are of a variety of sizes, but yet in general so nicely graded as to form an almost regular series from smallest to largest. A second glance, however, reveals the fact that there is one very prominent break in this graded series, separating the six smaller chromosomes from the remaining larger ones, and a count of the larger group shows it to contain seventeen units, giving as a total the odd number twenty-three.⁴ The odd or twenty-third member of the group, as can be plainly seen in the following division, is the accessory chromosome, which on account of its peculiar behavior will be considered separately. There is, therefore, in the ordinary group, the even number, twenty-two. More especially in the smaller group, but likewise in the members of the sixteen, it can be seen that the gradations in volume are not between individual chromosomes but between pairs, the two members of which in each case are of approximately equal size. In other words, there are, in the ordinary chromosome group, not twenty-two but eleven sizes of chromosomes. The lettering in the figure will indicate the pairs in the smaller group where they are most clearly defined.

Eight⁵ generations of spermatogonia follow this one, and in each succeeding metaphase the same number and size-relations of chromosomes may be observed. This is shown in Figs. 2 and 3, representing different secondary spermatogonial generations, in each of which appears six small chromosomes and seventeen larger ones. In each of these also, especially in the case of the smaller group, the members of which, on account of their nearly spherical form, do not suffer the same degree of foreshortening in the drawing as do many of their longer comrades — the paired relation may again be made out. Moreover, in the smaller group with its fewer members and greater size-differences, it is possible to see that the volume of the smallest pair (*kk*), for instance, in one cell bears approximately the same ratio to the homologous pair in another cell as does that of the largest (*jj*) of the first cell to the largest of the second, or the middle-sized pair (*ii*) of the one to the middle-sized pair of the other. In these cells the compact condition of the chromosomes will not permit of the accurate recognition of individual elements — other than perhaps the largest

⁴ Montgomery (*l.c.*) has found four of the Hemiptera-heteroptera to possess an odd somatic number of chromosomes and I have observed the same to be true for some fifty species of Acrididae and Tryxalinae.

⁵ Based on estimates of the number of cells in a spermatocyst at the time of transformation to spermatocytes.

and the smallest — in the group of sixteen, where size differences are comparatively slight, but this deficiency will be made up in the consideration of the group in the spermatocytes.

FIG. 2.

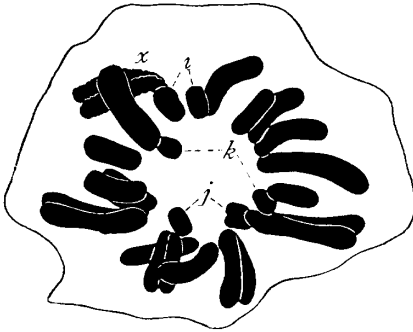


FIG. 3.

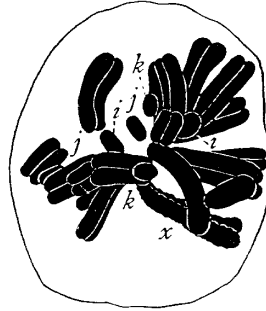


FIG. 2. Polar view of equatorial plate in secondary spermatogonium of one of the earlier generations. (From section.)

FIG. 3. Oblique lateral view of equatorial plate of a secondary spermatogonium of one of the later generations. (From a smear-preparation.) Small chromosomes and accessory designated as in Fig. 1.

Throughout all the secondary spermatogonia generations, in all stages except those of active division, the accessory chromosome remains apart in a vesicle which is virtually a separate nucleus. The genetic relation of the accessory chromosome of any secondary spermatogonium to that of any other in its line of ancestry seems, therefore, unquestionable. Each of the sixteen chromosomes of the larger group has also been enclosed in a separate vesicle (Fig. 4) during the period of metabolic activity, but these vesicles are practically always in communication with one another at their polar extremities, forming there a common compartment in which the six smaller units are frequently found. In this case there is plainly a possibility for an exchange of chromatic matter; but since each generation exhibits the same series of chromosomes as that before; and since, after the stages of the very fine spireme, the chromosomes reappear one in each sacculation as before, no other conclusion seems credible than that they are, chromosome for chromosome, the same in one generation as in another, just as is the case with the accessory.

FIG. 4.

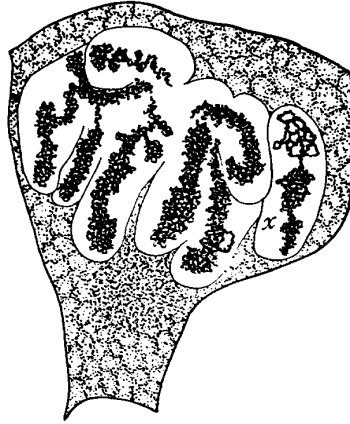


Fig. 4. Secondary spermatogonium in early prophase, showing very fine spiremes arranged in their respective diverticula of the nucleus. Most of the partition walls between diverticula are shorter in the figures than in the preparation, since their crossing if drawn in full would only cause confusion in a line drawing. (From a section.)

During the transformation to spermatocytes, the nucleus as a whole becomes spherical, but, in many cases, the compartments still remain; and in them the chromosomes pass through the fine spireme stages. In this condition, as in that just described for the spermatogonia, it is difficult to conceive the formation of a continuous spireme; but when, at a little later stage, cell and nuclear membranes have become less resistant so that their contents may be smeared upon cover-glasses and there fixed for study *in toto*, it becomes clear that fewer spiremes are present than in the spermatogonial nuclei. In every case, the accessory chromosome appears in its peculiar characteristic condition (*x*, Figs. 5*a*, 5*b*, 6 and 7), and careful counting of a large number of cases shows the spiremes in every favorable instance to number eleven. These spiremes are graded as to size just as were the chromosome-pairs of the spermatogonia — and the gap in the series separates a group of eight large from a group of three small elements. In most of the spiremes a longitudinal split is clearly visible, and in addition, in practically every case, a division may be noted separating the spireme into two distinct limbs of approximately equal size, which are frequently doubled on each other at the point of union.

FIG. 5a.

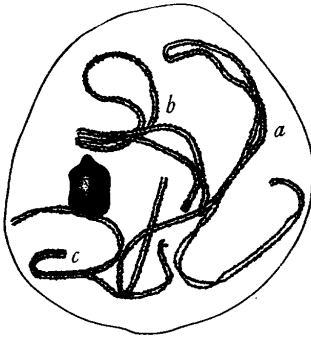


FIG. 5b.

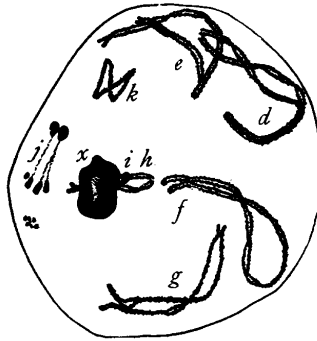


FIG. 5a. Three largest spiremes and accessory chromosome from a primary spermatocyte in early prophase. (Smear-preparation.)

FIG. 5b. Eight remaining chromosomes and accessory from same cell as Fig. 5a.

FIG. 6.

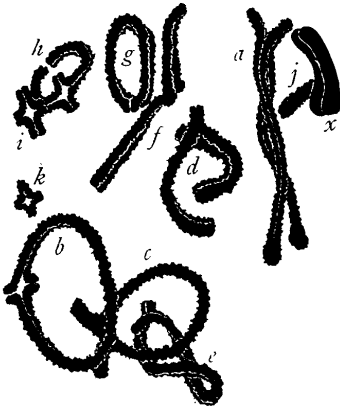


FIG. 7.



FIG. 6. Partly condensed spiremes in middle prophase of primary spermatocyte. All the chromosomes, including the accessory (*x*), show indications of a longitudinal split.

FIG. 7. Slightly more advanced chromosome group than that of Fig. 6. Letters *a*, *b*, *c*, *d*, *e*, *f*, *g*, *h*, *i*, *j* and *k* designate the different chromosomes in order of size from largest to smallest; *x* designates the accessory.

If now we seek the relation of these spiremes to the chromosomes of the spermatogonia, we find abundant data. Twenty-two chromosomes enclosed in separate compartments, each opening at one end into a common chamber are represented by eleven double chromosomes. Scarcely any two of the eleven are even approximately of the same size whereas each of the twenty-two appeared to have a mate of like volume. But the eleven double chromosomes are made up each of two limbs of equal size and we find it difficult to believe that these limbs do not represent the members of the pairs, joined together at their polar ends, which, as we have seen, projected into a common chamber of the nucleus. To such a conclusion additional weight is added by the occasional finding of telophases of the last spermatogonial generation which actually shows such a fusion (Fig. 8).

FIG. 8.

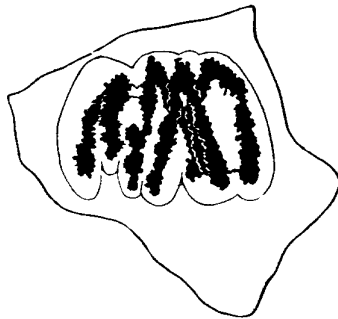


FIG. 8. Telophase of secondary spermatogonium of the last generation showing synapsis. Only a few of the chromosomes are shown and as in Fig. 4; to avoid confusion the sacculations are drawn only to the point where they cross one another.

The four parts of each spireme, marked off by the longitudinal split and the line of fusion, may be traced through aft the pro phases up to the metaphase, where they are clearly seen to become the four parts of the tetrad. These facts seem to me to leave no escape from the conclusion that in the completed tetrad the longitudinal split represents merely the usual division of a chromosome into equivalent chromatids; but *the transverse marking separates two spermatogonial chromosomes which have conjugated end-to-end in synapsis.*⁶

⁶ Cf Montgomery, T. H., Jr. (1901), "The Spermatogenesis of *Peripatus (Peripatopsis) Balfouri* up to the Formation of the Spermatid," *Zool.*

Notwithstanding the fact that no continuous spireme is formed, the various spiremes of the larger group (16 in spermatogonia, 8 in spermatocytes) in any nucleus are at any given period always of approximately the same diameter and the same degree of concentration. Their respective lengths may therefore be taken as a measure of their respective volumes, and accordingly the longer and more slender the spiremes, the more pronounced their differences of volume would appear. Obviously, it is impossible to study the length of convoluted spiremes in sections. Smear preparations also fail in the spermatogonia on account of the strength of the nuclear membrane, which in these cells resists the roughest treatment and prevents the separation of its contained spiremes. But in the prophases of the primary spermatocytes the nuclear membrane becomes so thin and weak that its contents may be readily smeared upon a cover-glass and the spiremes thus separated and to a certain extent flattened in the plane of the cover. In the most favorable of these cases, such as those shown in Figs. 5, 6 and 7, which represent different stages in the concentration of the spermatocyte spiremes, a more or less accurate comparison by means of measurements is possible. For the sake of convenience in reference, we will designate the chromosomes in these figures by the first eleven letters of the alphabet, beginning with the longest chromosome and proceeding according to size. The chromosomes as drawn are in all cases simple projections and hence suffer a greater or less amount of foreshortening according to the degree of their curvature or inclination to the plane of the slide. This, however, is so slight that it has been disregarded in the table except in case of chromosomes *b* and *h* of Fig. 6. In these cases, the actual length in the figure is given in parentheses and an estimate of the real length in the regular column. No attempt was made to measure the three smaller elements, as their variations in form and diameter in the spermatocytes render measurement in one dimension of no value whatever. Naturally these figures can make no pretensions to complete accuracy but as approximations they serve to show a uniformity in the different nuclei that cannot justly be ascribed to chance. It is worthy of note that the only case in which a chromosome does not bear approximately the same ratio as its mates to the homologous members of the other two series is chromosome *h* of Fig. 5; which, being hidden for the most part behind the accessory, is at best a doubtful quantity.

Jahrb., XV.; also "A Study of the Chromosomes of the Germ Cells of the Metazoa," *Trans. Amer. Phil. Soc.*, Vol. XX.

	Fig. 3.	Fig. 6.	Fig. 7.
<i>a</i>	43	22	21
<i>b</i>	32½	19½ (17)	17
<i>c</i>	23	15½	15
<i>d</i>	20	14	12
<i>e</i>	17½	12½	9
<i>f</i>	16½	10 2/3	7 2/3
<i>g</i>	15	9	7½
<i>h</i>	(7½)	8½ (7 2/3)	7
<i>i</i>			
<i>j</i>			
<i>k</i>			

NOTE. — THE FIGURES ARE IN TERMS OF AN ARBITRARY UNIT EQUIVALENT TO THE DISTANCE APART OF THE DIVIDER-POINTS USED IN MAKING THE MEASUREMENTS.

When the ordinary chromosomes divide in the first mitosis of the spermatocytes, the separation takes place along the line of the longitudinal split and therefore, except that the chromosomes are joined together by pairs, differs in no respect from an ordinary spermatogonial division. The accessory chromosome, however, though showing a clearly-defined longitudinal split, *does not divide but passes entire to one pole*, as Sinéty⁷ has independently observed in the Phasmidae; and after completion of the division may be clearly seen in one only of the two daughter cells, where it is sharply contrasted with the partially disintegrated ordinary chromosomes.

In the prophases of the second division the chromosomes reappear in the same number and show the same size relation as in the preceding telophase, but instead of exhibiting a longitudinal split *they are seen to be composed of two equal limbs joined together at one end only (Fig. 9) just as when they passed to the pole in the previous anaphases*. The division occurs at the point of junction of the two limbs and is unquestionably transverse — *separating the two chromosomes at the point where they fused in synapsis two generations before*.

⁷ Sinéty, R. de (1901), "Recherches sur la biologie et l'Anatomie des Phasmes," *La Cellule*, T. XIX.

FIG. 9.

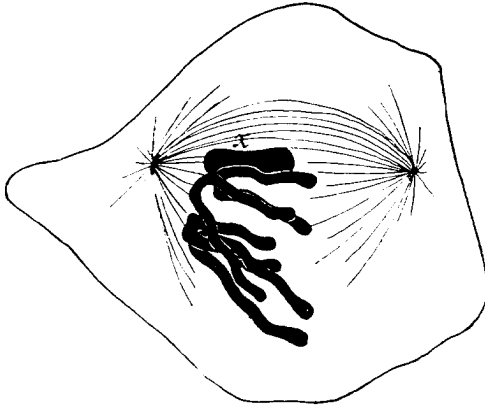


FIG. 9. Four ordinary chromosomes and accessory from a very late prophase of the secondary spermatocyte division. Each ordinary chromosome is made up of two limbs connected at one end. There is no longitudinal split.

In those secondary spermatocytes in which the accessory chromosome occurs, this element also divides, but in the line of the longitudinal split which has persisted from the prophases of the primary generation. One half of the resulting spermatids, therefore, are characterized by the presence of the accessory and the other half by its absence, but this constitutes the only morphological difference between the two categories. In each, the ordinary chromosomes may be seen to constitute a graded series of eleven members in which a considerable gap at one point separates a subgroup of three small units from another subgroup of eight larger ones (Fig. 10). The series therefore represent exactly half of the ordinary chromosome group as we found it throughout the secondary spermatogonia. This is the chromosome series which forms the chromatic portion of the spermhead and consequently is to be regarded *a priori* as the series which will reappear in the sperm-nucleus in the act of fertilization. If this is true — and everything speaks for and nothing definitely against the correctness of the assumption — then the conclusion seems unavoidable that the mate to each of the eleven chromosomes must be furnished by the egg-nucleus to produce the eleven pairs characteristic

of all the early germ-cells, of the follicle-cells of the ovary as shown by Fig. 11, and probably also of the ordinary somatic cells.⁸

FIG. 10.

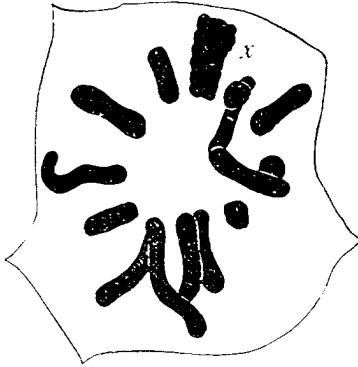


FIG. 11.



Fig. 10. Polar view of chromosome group in metaphase of secondary spermatocyte containing the accessory chromosome. Eight large and three small ordinary chromosomes appear. (From section.)

FIG. 11. Axial view of chromosome group of ovarian follicle-cell in telophase. Twenty-two chromosomes appear of which six are decidedly small and the other sixteen decidedly larger.

To sum up, in *Brachystola* the nuclei, not only of the presynaptic germ cells, but also of cells which have been shunted off from the germinal cycle are characterized by the possession of a chromosome group made up of two morphologically equivalent series of eleven members each.⁹ Comparison shows that the size-relations between various members of these series are approximately the same in different nuclei of the same or different cell generations. The numerical reduction (pseudo-reduction) is accomplished by the union of homologous members of the two series of a nucleus, and this union

⁸ Cases of cells other than germ-cells in which an accurate count of the chromosomes is possible are extremely rare on account of the crowded condition of their nuclei; but I am able to state that in the cells of the ovarian follicles and of the common collecting ducts of the testes every division figure shows large and small chromosomes in apparently the same relation as those found in the spermatogonia.

⁹ Besides the accessory chromosome.

is terminated in the second spermatocyte division by the separation of the daughter-chromosomes of the original conjoints at their point of union and their passage to opposite poles. We are virtually able to recognize each chromosome in eleven consecutive cell-generations; and in the prophases and telophases of nine of these, the chromosomes are separated from one another for a great part of their length, only their polar ends lying in the common chamber. No continuous spireme is formed; and although after each division there is a brief interval, during which chromosomic boundaries can no longer be traced, the regular correspondence, unit for unit, of the mother series with the daughter series establishes a high probability that we are dealing with morphologically distinct individuals, each of which bears to its mother element a genetic relation comparable to that existing between mother and daughter cells.

I have endeavored to show that the eleven ordinary chromosomes which enter the nucleus of each spermatid are selected one from each of the eleven pairs which made up the double series of the spermatogonia. It now becomes a highly interesting question whether there exists in the ripe egg a graded series of chromosomes similar to that of the mature male element. I have found the chromosome group not only of the oögonia but also of the ovarian follicle cells (Fig. 11) to correspond perfectly with that of the spermatogonia; and if we are permitted to assume that the reduction process in both sexes is the same, we have no alternative but to believe that the chromosome series of the mature germinal products also are alike. Obviously, copulation of such nuclei in fertilization would restore the conditions which we have found not only in the early germ-cells but in some outside the line of succession.

These latter observations have totally disregarded the accessory chromosome, but it is in it, if further research shall substantiate my present limited but thoroughly consistent results, that we shall find our most unequivocal evidence of chromosomic individuality. We have noted that the spermatogonia have twenty-three chromosomes, and that the odd one of these is the accessory which by means of its idiosyncrasies may readily be recognized in all except the active mitotic stages. We have also noticed that this element is unequally distributed in the maturation divisions and as a consequence occurs in exactly half the spermatozoa. In the oögonia and ovarian follicle-cells in which I have been able to count the chromosomes, I have found but twenty-two; and the fact that none of these behaves in the characteristic manner of the accessory proclaims it the missing member.

We should expect therefore to find but one kind of mature ova in respect to number of chromosomes while we know that by the same standard there are two kinds of spermatozoa. Obviously, then, the number of chromosomes in the cleavage-nucleus of the fertilized egg (twenty-two or twenty-three) must depend upon the number introduced in the sperm-nucleus, since the latter contains either eleven or twelve, according as the accessory chromosome is absent or present. Now twenty-three is the number of chromosomes in the male cells, while twenty-two is the number I have found in the female cells, and thus we seem to find a confirmation of McClung's¹⁰ suggestion that the accessory chromosome is in some way concerned in the determination of sex.

Without discussing here the logical consequences of such a conclusion, I will only emphasize the fact that one of the chromosomes, which in the primary spermatogonia is scarcely distinguishable from its fellows, maintains throughout a long series of divisions an indubitable independence; and finally completely establishes its right to the title of a distinct individual by passing entire to one daughter-cell with the result that no accessory chromosome appears in the products of the next division of the other.

Taken as a whole, the evidence presented by the cells of *Brachystola* is such as to lend great weight to the conclusion that a chromosome may exist only by virtue of direct descent by longitudinal division from a preëxisting chromosome and that the members of the daughter group bear to one another the same respective relations as did those of the mother group — in other words, that the chromosome in *Brachystola* is a distinct morphological individual.

This conclusion inevitably raises the question whether there is also a physiological individuality, *i.e.*, whether the chromosomes represent respectively different series or groups of qualities or whether there are merely different-sized aggregations of the same material and, therefore, qualitatively alike.

On this question my observations do not furnish direct evidence. But it is *a priori* improbable that the constant morphological differences we have seen should exist except by virtue of more

¹⁰ McClung, C. E., "Notes in the Accessory Chromosome," *Anat. Anz.*, XX.; "The Accessory Chromosome, Sex-determinant," *Biol. Bull.*, III. 2 A study of the chromosomes of the primary spermatogonia has been made in *Melanoplus differentialis*, a nearly related form in which the later divisions are essentially the same as in *Brachystola*.

fundamental differences of which they are an expression; and, further, by the unequal distribution of the accessory chromosome we are enabled to compare the developmental possibilities of cells containing it with those of cells which do not. Granting the normal constitution of the female cells examined and the similarity of the reduction process in the two sexes, such a comparison must show that this particular chromosome does possess a power not inherent in any of the others — the power of impressing on the containing cell the stamp of maleness, in accordance with McClung's hypothesis.

The evidence advanced in the case of the ordinary chromosomes is obviously more in the nature of suggestion than of proof, but it is offered in this connection as a morphological complement to the beautiful experimental researches of Boveri¹¹ already referred to. In this paper Boveri shows how he has artificially accomplished for the various chromosomes of the sea urchin, the same result that nature is constantly giving us in the case of the accessory chromosome of the Orthoptera. He has been able to produce and to study the development of blastomeres lacking certain of the chromosomes of the normal series.¹² In larvae resulting from double-fertilized eggs which have divided into three cells at the first cleavage, he recognizes an organism made up of definite thirds, each traceable to one of the original blastomeres and each characterized, as a result of the primary hap-hazard tripolar division, by a different combination and generally by a different number of chromosomes from that of its fellows. In rare instances such an embryo may be normal, of which fact the possibility that each pole of the triaster may receive a complete normal series of chromosomes is explanation enough. In other cases, the embryo may be completely normal (for instance in respect to skeleton or pigmentation) in one or two thirds, while in the remaining portion these structures may be entirely lacking; and it is a most significant fact that "in einzelnen dieser Fälle konnte aus der Kerngröße nachgewiesen werden, dass die Grenze wo der Defekt beginnt, mit der Grenze zweier auf verschiedene Ausgangsblastomeren

¹¹ Boveri, *l. c.*

¹² By the normal series is here meant such a one as occurs in the nucleus of either of the mature germinal products, since it has been clearly shown by the well-known work on the fertilization of enucleate egg-fragments and on chemically induced parthenogenesis, that either of the ripe germ-products possesses all the chromatin necessary for the production of a normal larva.

zurückführender Bereiche zusammenfällt." In the "normal" embryos mentioned above, every part was present, and as regards specific characters, normal but in different thirds there could be seen individual variations which normally should have appeared in different larvae. "In der That," says Boveri, "könnte ich aus den verschiedenen Typen der normalen Kontrolzuchten, durch Kombination der rechten Hälfte einer Larve mit der linken einer anderen, Bilder herstellen, die den in Rede stehenden Dreierplutei fast genau entsprechen." To these points is added the fact that while all the isolated blastomeres of a normal four-cell stage develop exactly alike, those of dispermic three- or four-cell stages rarely or never do so, even when the numerical distribution of chromosomes appears equal; and, further, that in large numbers of larvae from double-fertilized eggs all possible combinations of characters are to be found, just as all possible combinations of chromosomes from the three parent cells may enter into the composition of their nuclei. From these and other data, Boveri draws the conclusion that "Nicht eine bestimmte Zahl sondern eine bestimmte Kombination von Chromosomen zur normalen Entwicklung notwendig ist, und dieses bedeutet nichts anders als dass die einzeln Chromosomen verschiedenen Qualitäten besitzen müssen."

Thus we are brought to recognize a physiological individuality in a form in which the chromosomes are morphologically indistinguishable and the nuclei of which, after the anaphases, offer no mechanical hindrance to the free intermixture of the chromatin. We have already reviewed the reasons for believing the accessory chromosome in the cells of *Brachystola* to be the possessor of specific functions and it only remains again to call attention to the likelihood that the constant morphological differences between the ordinary chromosomes are the visible expression of physiological or qualitative differences,

In conclusion, from the point of view thus suggested, let us again consider the phenomena of fertilization. In either sperm- or egg-nucleus a complete series must be present since either may produce a normal embryo without the other. Every normal fertilized egg, therefore, as well as every cleavage-cell derived from it, must have the field of each character covered by two chromosomes — one from each parent. The chromosome series of the echinoderm cleavage-nucleus is thus shown to be physiologically a double one just as in *Brachystola* we have seen it to be morphologically double, and the doubling in both cases is seen to be accomplished in an exactly

similar way — viz., by the contribution of equivalent series by the two parents.

If, as the facts in *Brachystola* so strongly suggest, the chromosomes are persistent individuals in the sense that each bears a genetic relation to one only of the previous generation, the probability must be accepted that each represents the same qualities as its parent element. A given relative size may therefore be taken as characteristic of the physical basis of a certain definite set of qualities. But each element of the chromosome series of the spermatozoon has a morphological counterpart in that of the mature egg and from this it follows that the two cover the same field in development. When the two copulate, therefore, in synapsis¹³ the entire chromatin basis of a certain set of qualities inherited from the two parents is localized for the first and only time in a single continuous chromatin mass; and when in the second spermatocyte division, the two parts are again separated, one goes entire to each pole contributing to the daughter-cells the corresponding group of qualities from the paternal or the maternal stock as the case may be.

There is, therefore, in *Brachystola* no qualitative division of chromosomes but only a separation of the two members of a pair which, while coexisting in a single nucleus, may be regarded as jointly controlling certain restricted portions of the development of the individual. By the light of this conception we are enabled to see an explanation of that hitherto problematical process, synapsis, in the provision which it makes that the two chromosomes representing the same specific characters shall in no case enter the nucleus of a single spermatid or mature egg.

I may finally call attention to the probability that the association of paternal and maternal chromosomes in pairs and their subsequent separation during the reducing division as indicated above may constitute the physical basis of the Mendelian law of heredity. To this subject I hope soon to return in another place.

I take pleasure in expressing here my gratitude to Prof. E. B. Wilson for much valuable advice and assistance in the work upon *Brachystola* and in the preparation of the present paper.

¹³ The suggestion that maternal chromosomes unite with paternal ones in synapsis was first made by Montgomery (1901, 1.).